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Jon E. Keeley and Sterling C. Keeley

Made in United States of America
Reprinted from Madroño
Vol. 34, No. 3, July–September 1987

ROLE OF FIRE IN THE GERMINATION OF CHAPARRAL HERBS AND SUFFRUTESCENTS

JON E. KEELEY
Department of Biology, Occidental College,
Los Angeles, CA 90041

STERLING C. KEELEY
Department of Biology, Whittier College,
Los Angeles, CA 90608

ABSTRACT

Fifty-seven herbaceous and suffrutescent species common after fire in chaparral were tested for their response to charred wood and heat shock of 120°C for five minutes. Over half of the species germinated readily without either treatment. These included all of the herbaceous perennial monocots, most herbaceous perennial dicots, and a number of annuals. In most species, the heat treatment reduced germination and only one species was stimulated significantly by heat. Forty-two percent of the species showed significant enhancement of germination with charred wood. For some perennials, such as *Penstemon spectabilis* and *Romneya coulteri,* and an annual, *Papaver californicum,* there was a near obligatory requirement for charred wood. Significant enhancement of germination in the presence of charred wood is now known for species in 10 plant families: Asteraceae, Boraginaceae, Brassicaceae, Caryophyllaceae, Hydrophyllaceae, Onagraceae, Papaveraceae, Polemoniaceae, Rubiaceae, and Scrophulariaceae. Several fire-following species, *Eucrypta chrysanthemifolia* and *Dicentra* spp., failed to germinate under any treatment.

Since the early observations of Brandegee (1891), botanists have been impressed by the often spectacular wildflower displays that occur the first growing season after wildfire in chaparral. Over 200 species of annuals, herbaceous perennials, and short-lived suffrutescents have been recorded from chaparral burns. This abundance and diversity of herbs is in marked contrast to the generally depauperate herbaceous vegetation in mature chaparral (Sweeney 1956, Stocking 1966, Keeley et al. 1981).

Nearly all of this temporary vegetation arises from seed or vegetative parts present in the soil prior to burning. This fact has resulted in two theories accounting for the breaking of seed dormancy after fire: 1) seeds are inhibited from germinating by the mature chaparral vegetation (allelopathy) and fire releases seeds from this inhibition, or 2) seed germination is stimulated by fire.

The question of allelopathic inhibition of seeds by chaparral has been examined in numerous studies (Sweeney 1956, McPherson and Muller 1969, Christensen and Muller 1975a,b, Kaminsky 1981, Keeley et al. 1985), but its role in inhibiting seed germination is unclear.

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There is strong evidence, however, that many chaparral species have seeds that, under natural conditions, require a stimulus from fire for germination. Germination of some species is stimulated by heat shock from fire that ruptures the seed coat (Sweeney 1956, Christensen and Muller 1975a,b, Keeley et al. 1985). Germination of other fire-following herbs is stimulated by a chemical leached from charred (but not ashed) wood (Wicklow 1977, Jones and Schlesinger 1980, Keeley et al. 1985). Many species have been tested for their germination response to heat shock; however, the vast majority of chaparral herbs and suffrutescents have not been tested for their response to charred wood.

Although germination of many chaparral species is apparently dependent upon one or the other of these fire-related cues, a number of species are known to germinate readily without such cues (e.g., Sweeney 1956, Keeley et al. 1985).

The purpose of this study was to test the germination response of 57 species, representing all of the life-histories and growth forms present in the temporary postfire vegetation. Specific questions addressed were: 1) How widespread is charred wood stimulated germination? 2) For species with charred wood stimulated germination, will heat shock produce a similar stimulation in germination? 3) To what extent can generalizations be drawn concerning the relationship of growth form and germination response?

Methods

Selection of species was based on availability of plants with mature seed crops that were present in recently burned chaparral. Collections were made between elevations of 500–1500 m in Los Angeles, Riverside, San Diego, San Bernardino and Ventura cos., California. Vouchers have been deposited at LOC (Occidental College). Nomenclature is according to Munz (1974). Seeds of each species were collected from a single population of 25 or more plants during the spring and summer of 1982 and stored in paper bags under room conditions for 14–18 months. Although there is little data on seed longevity of these species, the fact that many species may be absent on a site for decades prior to fire suggests the seed pool in the soil is quite long-lived (Sweeney 1956).

Seeds were sown into 60 × 15 mm petri dishes filled with 15 g (fresh weight) of commercial potting soil (Gro-Lite, see Keeley 1984 for chemical analysis of this soil). Charred wood was made by charring (but not ashing) 1–2 cm diameter stems of the chaparral shrub *Adenostoma fasciculatum* and grinding in a Wiley Mill to pass a 1 mm screen. Charred wood treatments received 0.5 g of this powdered charred wood. For comparison, a heating treatment of seeds was included. The treatment of 120°C for five minutes was selected be-

TABLE 1. GERMINATION OF SELECTED CHAPARRAL HERBS AND SUFFRUTESCENTS IN RESPONSE TO 120°C FOR FIVE MINUTES OR APPLICATION OF POWDERED CHARRED WOOD TO THE GERMINATION MEDIUM (N = 5 DISHES OF 50 SEEDS EACH). A = annual, B = biennial, Hp = herbaceous perennial, S = suffrutescent, * = non-native. # = *Gilia capitata* seeds from two populations were tested, a first year burn and an adjacent mature chaparral stand. ns = no significant difference between treatments (p > 0.05); for species with significant difference, treatments with the same superscript are not significantly different at p > 0.05.

		Percentage germination			
	Growth form	Control	120°C 5 min	Charred wood	p
Dicots					
Apiaceae					
Daucus pusillus	(A)	30	10[a]	18[a]	<0.01
Lomatium dasycarpum	(Hp)	12	1	4	<0.01
Asteraceae					
Agoseris heterophylla	(A)				
Beaked achenes		79	86	88	ns
Non-beaked achenes		62	78	92	<0.001
Gnaphalium californica	(A/B)	46[a]	67[a,b]	79[b]	<0.05
Heterotheca grandiflora	(A/B)	91[a]	44	86[a]	<0.001
Lactuca serriola	(A*)	53	44	54	ns
Madia gracilis	(A)	86[a]	45	86[a]	<0.05
Malacothrix clevelandii	(A)	9[a]	10[a]	35	<0.001
Microseris linearifolia	(A)	98	96	95	ns
Perezia microcephala	(Hp)	35	1	9	<0.001
Porophyllum gracile	(S)	72[a]	26	73[a]	<0.01
Rafinesquia californica	(A)	4[a]	3[a]	55	<0.01
Stephanomeria virgata	(A)	45[a]	40[a]	56	<0.05
Boraginaceae					
Cryptantha intermedia	(A)	55[a]	55[a]	74	<0.05
Brassicaceae					
Lepidium nitidum	(A)	2[a]	3[a]	22	<0.001
Sisymbrium orientale	(A*)	94	79[a]	74[a]	<0.01
Streptanthus heterophyllus	(A)	1[a]	7[a]	25	<0.001
Caryophyllaceae					
Silene gallica	(A*)	64[a]	66[a]	34	<0.01
S. multinervia	(A)	6[a]	9[a]	44	<0.01
Fabaceae					
Lotus salsuginosus	(A)	6[a]	24[a]	2	<0.01
L. strigosus	(A)	35[a]	38[a]	24	<0.05
Hydrophyllaceae					
Eucrypta chrysanthemifolia	(A)	0	0	0	ns
Phacelia minor	(A)	0[a]	0[a]	13	<0.001
Onagraceae					
Camissonia californica	(A)	3[a]	6[a]	49	<0.001

TABLE 1. CONTINUED.

	Growth form	Percentage germination: Control	120°C 5 min	Charred wood	p
Clarkia epilobioides	(A)	42[a]	54[a]	75	<0.001
C. purpurea	(A)	40[a]	40[a]	72	<0.05
C. unguiculata	(A)	61	65	68	ns
Papaveraceae					
Dicentra chrysantha	(Hp)	0	0	0	ns
D. ochroleuca	(Hp)	0	0	0	ns
Papaver californicum	(A)	0[a]	0[a]	89	<0.001
Romneya coulteri	(S)	0[a]	0[a]	40	<0.001
Polemoniaceae					
Gilia australis	(A)	31[a]	32[a]	80	<0.001
G. capitata	(A)				
Mature chaparral#		8[a]	22[a]	83	<0.001
Burned chaparral#		20[a]	25[a]	69	<0.001
Polygonaceae					
Chorizanthe fimbriata	(A)	37	29	45	ns
Pterostegia drymarioides	(A)	68	30	47	<0.01
Ranunculaceae					
Delphinium cardinale	(Hp)	50[a]	2	40[a]	<0.001
D. parryi	(Hp)	68[a]	30	61[a]	<0.0
Rubiaceae					
Galium angustifolium	(Hp/S)	22	17	43	<0.001
G. parisiense	(A*)	85	89	100	ns
Scrophulariaceae					
Antirrhinum coulterianum	(A)	2[a]	3[a]	42	<0.001
A. kelloggii	(A)	39[a]	45[a]	63	<0.01
A. nuttallianum	(A)	69	56	58	ns
Collinsia parryi	(A)	24	12	77	<0.001
Cordylanthus filifolius	(A)	57[a]	27	62[a]	<0.05
Penstemon centranthifolius	(Hp)	0[a]	2[a]	16	<0.001
P. heterophyllus	(Hp)	54	4	74	<0.001
P. spectabilis	(Hp)	1[a]	3[a]	61	<0.001
Scrophularia californica	(Hp)	82[a]	67[a]	25	<0.001
Solanaceae					
Solanum douglasii	(S)	82[a]	85[a]	63	<0.01
Amaryllidaceae					
Allium praecox	(Hp)	18	14	18	ns
Bloomeria crocea	(Hp)	55	46	60	ns
Dichelostemma pulchella	(Hp)	100	1	64	<0.001

Table 1. Continued.

	Growth form	Percentage germination			
		Control	120°C 5 min	Charred wood	p
Liliaceae					
Calochortus concolor	(Hp)	84[a]	66	82[a]	<0.05
C. splendens	(Hp)	89	9	66	<0.001
Chlorogalum parviflorum	(Hp)	46	15	46	<0.01
Poaceae					
Melica imperfecta	(Hp)	42	51	34	ns
Stipa lepida	(Hp)	77	64	64	ns

cause it stimulates germination of many chaparral herbs (Keeley et al. 1985). Seeds were heated in a forced convection oven prior to sowing. For both treatments and a control, in which seeds were not heated and charred wood was not applied, five replicate petri dishes of 50 seeds each were tested. The experiment was initiated by addition of 8 ml of deionized water to all dishes except charred wood treatments, which received 10 ml because of water absorption.

Seeds of some species require a period of low temperature treatment in order to overcome embryo dormancy. Periods of two weeks to two months are commonly employed (Atwater 1980), with the longer periods being required for species from higher elevations and latitudes. Many chaparral species from southern California do not require stratification (J. Keeley, unpubl. data). In this investigation, stratification requirement was not studied; however, all dishes were maintained at 5°C for three weeks prior to incubation at 23°C for two weeks, under a 12 hour photoperiod at approximately 350 μmol m^{-2} s^{-1}. Germination was scored after the pre-chilling treatment and each week at 23°C. To determine if some species might require a longer cold treatment, this cycle of three weeks cold and two weeks at 23°C was repeated once before ending the experiment.

Treatments, including controls, were compared with 1-way ANOVA on arcsin transformed data and the Student-Newman-Keuls multiple range test.

Results

Fifty-seven herbs were tested for their response to charred wood and heat shock (Table 1). Two-thirds of the 22 herbaceous perennial and suffrutescent species germinated readily under 'control' conditions and showed no enhancement with either treatment. These included all of the monocot species tested. The heat treatment of 120°C for five minutes did not stimulate germination of any of the herbaceous perennials, but the possibility of seeds being stimulated by other heating treatments cannot be ruled out. Heating, however, tended to reduce germination of many herbaceous perennials. In these species, heating was apparently lethal because many of the seeds had rotted by the end of the experiment. Germination of five herbaceous perennial and suffrutescent species was stimulated significantly by charred wood; this response was particularly striking in *Penstemon spectabilis* and *Romneya coulteri,* but also was observed in *Galium angustifolium, Penstemon centranthifolius,* and *P. heterophyllus.*

Germination of 20 of the annual species was enhanced significantly by charred wood (Table 1). Some species, e.g., *Papaver californicum* and *Phacelia minor,* showed a nearly complete dependence on charred wood. For other species, e.g., *Antirrhinum coulterianum, Camissonia californica, Gilia capitata, Lepidium nitidum, Rafinesquia californica, Silene multinervia,* and *Streptanthus heterophyllus,* the presence of charred wood resulted in nearly an order of magnitude greater germination. In others, such as *Agoseris heterophylla, Antirrhinum kelloggii, Collinsia parryi, Clarkia* spp., *Cryptantha intermedia, Gilia australis, Gnaphalium californica, Malacothrix clevelandii,* and *Stephanomeria virgata,* there was often substantial 'control' germination, but an additional 20–50% germination with charred wood.

Heat treatment stimulated the germination of *Lotus salsuginosus,* but reduced the germination of seven other annuals, including species with charred wood stimulated germination. *Agoseris heterophylla* had polymorphic germination behavior related to achene morphology; non-beaked achenes had significantly greater germination with heat and charred wood treatments in contrast to the beaked achenes.

Several common fire-following species, *Dicentra chrysantha, D. ochroleuca,* and *Eucrypta chrysanthemifolia,* failed to germinate, despite having seeds that appeared filled and viable (tetrazolium testing was inconclusive due to the very small or rudimentary embryos characteristic of these species).

Timing of germination was variable and not related clearly to growth form or germination response. For example, 90% of the total germination of *Calochortus splendens,* an herbaceous perennial, had occurred by the end of the three week pre-chilling treatment; this pattern also was observed for *Dichelostemma pulchella* and annuals such as *Gilia capitata, Heterotheca grandiflora, Pterostegia drymarioides,* and *Rafinesquia californica.* Other herbaceous perennials, e.g., *Allium praecox, Bloomeria crocea, Chlorogalum parviflorum, Penstemon spectabilis* and *Scrophularia californica,* and annuals such as *Silene multinervia* and *Stephanomeria virgata* failed to germinate in the cold, but the vast majority germinated within the first week at 23°C. Some species (*Lotus strigosus* and *Silene gallica*) had more or less equal germination percentages at each scoring period throughout the 10 weeks. *Delphinium cardinale* was particularly slow to germinate, none germinated until the second cold treatment eight weeks after the beginning of the experiment.

Discussion

Germination behavior of fire-following herbs and suffrutescents can be categorized into species with no apparent dormancy (except perhaps a cold 'stratification' requirement) or ones with varying degrees of dormancy that can be overcome, under natural conditions, only by fire-related stimuli such as heat shock or charred wood.

Species with non-dormant seeds. Chaparral species with non-dormant seeds include all herbaceous perennial monocot species, both bulb-forming geophytes and bunch grasses, and many herbaceous perennial dicots, such as *Delphinium* spp., *Lomatium* spp., *Marah macrocarpus, Paeonia californica, Perezia microcephala,* and *Scrophularia californica* (Table 1; also Sweeney 1956, Everett 1957, Emery 1964, Keeley et al. 1985). The presence of these species on recently burned sites is the result of resprouting from underground vegetative parts; seedlings are uncommon at this time. Unlike most perennials that colonize burned sites via seedlings, these resprouting herbs flower vigorously during the first growing season after fire. We predict that the timing of seedling establishment is most likely in subsequent years after fire and up until the time the area is dominated by shrubs. These species survive in gaps in the shrub cover or under the canopy as dormant bulbs that occasionally produce depauperate growth, but seldom flower (Stone 1951, Stocking 1966, Christensen and Muller 1975a).

Non-dormant seeds also are characteristic of some annual species found commonly on burned sites. Some of these, such as *Agoseris heterophylla, Galium parisiense, Heterotheca grandiflora, Lactuca serriola,* and *Microseris linearifolia* (Table 1), are relatively weedy and produce diaspores capable of distant dispersal. Their presence on first-year burns can be accounted for by colonization from nearby disturbed areas such as road-cuts or natural disturbances. Many of these annuals have heat sensitive seeds and, thus, it is of interest that several disperse seeds in the fall and winter, after the time of most chaparral wildfires. Some of these species produce polymorphic achenes with different germination responses (e.g., *Agoseris heterophylla,* see Table 1, and *Heterotheca grandiflora,* see Flint and Palmblad 1978) that may promote colonization of burned sites.

Other less weedy, annual species also have non-dormant seeds. *Antirrhinum nuttallianum, Clarkia unguiculata, Cordylanthus filifolius, Madia gracilis, Pterostegia drymarioides* (Table 1), and *Festuca megalura* (Keeley et al. 1985) are often abundant in gaps in the mature canopy. The seeds of these species are dispersed during the summer dry season and do not germinate until the following winter wet season. Their presence on burned sites may be from seeds in the soil that were produced by 'gap' plants the previous season or from seeds under the canopy that, due to allelopathic compounds from the shrub overstory, were dormant prior to the fire.

Species with heat-stimulated germination. Lotus salsuginosus was the only species in this study with a significant increase in germination following heat treatment (Table 1). Other studies have reported heat-stimulated germination for annuals such as *Apiastrum angustifolium, Brassica nigra,* and *Camissonia hirtella,* as well as for suffrutescents such as *Helianthemum scoparium* and *Lotus scoparius* (McPherson and Muller 1969, Christensen and Muller 1975a, Keeley et al. 1985), and some shrubs such as *Ceanothus* spp. (Quick 1935). These species commonly are described as being 'hard-seeded' due to the heavily sclerified seed coats and thick cuticle that hinders imbibition (Atwater 1980). Heat melts or cracks the cuticle, commonly around the hilum or strophiole, and this is sufficient to allow germination because artificial scarification of the seed coat will produce the same stimulatory effect as heating. High soil temperatures may produce the same stimulus as a heat shock during fire and, thus, germination may be stimulated in gaps in the mature canopy as well as on disturbed sites.

Species with charred wood stimulated germination. Germination stimulated by charred wood is a far more specific means of timing seedling establishment to burned sites than is heat. Not surprisingly, such species are strongly associated with burns; sometimes they appear in abundance the first year after fire and then disappear until the next fire (true 'pyrophyte endemics'). Charred wood stimulated germination is widespread in the Hydrophyllaceae. It was first discovered in *Emmenanthe penduliflora* (Wicklow 1977) and later in many species of *Phacelia* (Keeley et al. 1985) and the shrub *Eriodictyon crassifolium* (Keeley 1987). In terms of environmental cues that they are likely to encounter in the field, these species exhibit a nearly complete dependence upon charred wood. Complete dependence upon charred wood also is found in both annual and perennial species of Papaveraceae (Table 1). Other families with species having a significant level of germination stimulated by charred wood include the Asteraceae, Boraginaceae, Brassicaceae, Caryophyllaceae, Onagraceae, Polemoniaceae, Rubiaceae, and Scrophulariaceae (Table 1). Some of these species, e.g., the annual *Gilia capitata* (Table 1), may persist in gaps during fire-free periods and produce seeds that are polymorphic in their germination response. A fraction of the seeds germinate each year and a larger portion remain dormant until after fire when germination is stimulated by charred wood (see also Grant 1949).

Based on the taxonomic distribution of germination responses observed here, we suggest that the mechanism behind germination stimulated by charred wood is different than that for germination stimulated by heat. Species in these two groups differ in several respects. Unlike seeds that are stimulated by heat shock, which have a smooth thick cuticle impermeable to water, seeds stimulated by charred wood have highly sculptured, reticulate seed coats that are not cutinized heavily. *Emmenanthe penduliflora,* for example, produces dormant seeds that will imbibe water (Sweeney 1956). Thus, it seems probable that the chemical leached from charred wood (apparently an oligosaccharide, Keeley and Pizzorno 1986) acts on some internal component, and affects gas permeability of membranes or provides a chemical stimulus to embryo development. The former hypothesis is supported by the fact that scarification will produce the same effect as charred wood (Wicklow 1977). The latter hypothesis is supported by the fact that artificial application of gibberellic acid can duplicate the charred wood stimulus. For example, germination of *Penstemon spectabilis* and *Romneya coulteri* increased from 1–61% and from 0–40%, respectively, in the presence of charred wood (Table 1) and Atwater (1980) reported increases from 2–70% for *P. spectabilis* and from 0–42% for *R. coulteri* with the addition of gibberellic acid.

Future research will focus on those fire-following species, e.g., *Eucrypta chrysanthemifolia, Dicentra crysantha, D. ochroleuca* (Table 1), and *Phacelia brachyloba* (Keeley et al. 1985), that we have been unable to germinate. All of these species are restricted largely to postfire conditions. Atwater (1980) has found that germination of *D. crysantha* can be accomplished with the addition of gibberellic acid. In light of the fact that in other species gibberellic acid can simulate the effect of charred wood, it is likely that under natural conditions, germination of these species is also cued by charred wood, but apparently in conjunction with some other unknown factor.

Acknowledgments

This work was supported in part by NSF grant RII-8304946. We thank Susan Conard and Richard Minnich for helpful comments on the manuscript.

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(Received 8 Feb 1986; revision accepted 22 Dec 1986.)